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THE DISCOVERY AND NAMING OF THE GENUS NYSSA

RICHARD H. EYDE

Nyssa is a small genus of woody plants, mostly trees, of eastern North America and southeastern Asia. The American nyssas, with which this paper is concerned, include *N. sylvatica*, found in forested areas throughout the eastern United States; *N. sylvatica* var. *biflora* and *N. uniflora*,[1] both dominant trees in inundated forests of the Coastal Plain; and *N. ogeche*, a species which is confined almost entirely to eastern Georgia and northern Florida. *N. biflora* is treated by some taxonomists as a separate species from *N. sylvatica*. *Nyssa* wood is of some slight commercial importance in the making of furniture, boxes, and paper pulp, and the nectar from flowers of *Nyssa ogeche* is a source for honey of excellent quality.

The fruits of *Nyssa* species are drupes of various sizes. The stone which each contains bears a distinctive valve which is pushed open by the root end of the growing embryo during germination of the single seed. The presence of this germination valve enables one to recognize a member of the genus in the absence of any plant part save the stony endocarp. Since *Nyssa* endocarps are easily preserved, as well as easily recognized, it is not surprising that this group of plants possesses a well established fossil record.

The occurrence of fossil *Nyssa* endocarps, and often *Nyssa* pollen, in divers Cenozoic strata of western North America, Japan, Siberia, England, and Central Europe leaves no doubt that *Nyssa*

[1] This is the *Nyssa aquatica* of Gray's *Manual*, 8th ed. (See Rickett, 1945)

trees formerly flourished in all temperate regions of the northern hemisphere. Evidence from many sources indicates that the range of this genus, like that of many others, gradually decreased during some tens of millions of years as a result of the long climatic cooling which preceded Pleistocene glaciation. The disappearance and later reappearance of *Nyssa* pollen at successively higher levels in early Pleistocene deposits of southern Poland (Szafer, 1954) show that nyssas had not been completely exterminated from that region at the end of the Pleistocene epoch and that they were able, moreover, to re-establish themselves from refugia during a warmer interval which followed the first onslaught of Pleistocene ice. Re-establishment was temporary, though, and *Nyssa* had become extinct in Europe by the time the last great glaciatian came to an end. With the retreat of the continental ice sheet, habitats favorable to the growth of these plants were restored. This assertion is corroborated by the observation of Franz Kirchheimer (1957, p. 570) that *Nyssa sylvatica* has propagated itself by seed in the vicinity of Heidelberg, Germany. The earliest occurrence of a member of the genus on European soil in recent time, however, was due to human agency, not to any migratory aptitude of the plant itself.

While engaged in research on the fossil ancestry of *Nyssa*, I became interested in the details of its discovery and subsequent introduction into Europe and in the origin of the name. The remarkable collection of original sources contained in the library at the Harvard University Herbarium has supplied information regarding these matters which is unavailable in later literature. The observations assembled in the present account are presented for the pleasure of any who, like myself, take delight in particulars from the history of botany.

THE FIRST DESCRIPTIONS AND COLLECTIONS OF NYSSA

Only a few of our American woody plants, e.g., *Thuja occidentalis*, were introduced into Europe at a very early date (Wein, 1930, 1931). This is doubtless due to the crassly exploitative attitude of the first adventurers to reach the New World. It is unbelievable that the vast numbers of *Nyssa* trees growing near

the Gulf of Mexico could have gone unnoticed by the 16th century Spanish explorers, but in their treasure-seeking the Spaniards had neither the time nor taste for collecting new and unusual plants or even for describing such plants in their journals. In scanning the writings of the first French settlers of Louisiana, I have likewise found little mention of trees and nothing at all relating to the genus *Nyssa*.

The intellectual atmosphere among the English of this period was quite different from that of their French and Spanish contemporaries. Visitors and settlers who could describe the climate, the geography, the ethnology, or the wildlife of the English colonies were encouraged to communicate their observations to members of the Royal Society for reading at the meetings of that young and vigorous organization. Accordingly, lists of New England plants were prepared during the 1600's by the visitor John Josselyn and by Governor Winthrop of Connecticut. The missionary John Banister of Virginia sent several notices of new plants to the "natural philosophers" back in London toward the end of the 17th century, and John Lawson, Surveyor General of North Carolina, compiled a delightfully perspicacious natural history of his own colony during the first decade of the 18th (Lawson, 1714).

Lawson included in his list of North Carolina trees and their uses a number of "Gum Trees". Following his description of "Sweet Gum" (clearly *Liquidambar*) we find this passage (p. 97-98):

> Of the Black Gum, there grows with us two sorts, both fit for Cart-Naves. The one bears a black, well tasted Berry, which the Indians mix with their Pulse and Soups, it giving them a pretty Flavour and Colour. . . . The other Gum bears a berry in shape like the others, though bitter and ill tasted. This Tree, (the Indians report) is never wounded by Lightning. It has no certain Grain, and it is almost impossible to split, or rive it.

I shall not attempt to identify the first of Lawson's black gums, but the second is surely a *Nyssa*, probably *Nyssa sylvatica* or *biflora*. These trees are still commonly called black gum or sour gum in reference to the color and taste of the fruits. The fourth and last of Lawson's gum trees is a "White Gum" which I cannot

recognize from his description, but it is not a *Nyssa*.

It is understandable that the zealous botanists of England could not long be satisfied with mere verbal descriptions and brief catalogues of New World plants. When Mark Catesby, while visiting his relatives in Virginia, sent actual specimens of plants to apothecary Samuel Dale of Essex, it caused such a stir among Dale's fellow collectors that they persuaded Catesby to make a second trip at their expense. Thus sponsored, Catesby traveled from 1722-1726 in Carolina, Florida, and the Bahamas, collecting and painting the wild things which he encountered.

Upon his return to England, Catesby published the descriptions and paintings which he had assembled. Volume I (1731) of this work contains readily recognizable illustrations of *Nyssa sylvatica* (plate 41) and *Nyssa uniflora* (plate 60), each of which is carefully described in French and in English. To these plants Catesby applied the names tupelo tree and water tupelo, respectively, the word tupelo being derived from the Indian name (Creek Indian for "swamp tree," according to *Webster's New International Dictionary*, 1957). These illustrations of Catesby's are the earliest pictures of *Nyssa*,[2] and it is likely that the Catesby collections in the Sloane Herbarium of the British Museum (Dandy, 1958) contain the first *Nyssa* specimens sent from the New World.

The eagerness with which the English received "curiosities" from America was fully shared by a number of Dutch enthusiasts. Perhaps the chief among these was Dr. J. F. Gronovius, Senator of Leyden. Gronovius' correspondence with the American collector John Clayton enabled him to obtain specimens and seeds of many plants previously unknown in Holland, and it was the Senator's practice to assign descriptive Latin polynomials to these new plants. When young Carl Linnaeus arrived in Leyden in 1735 with the manuscript of *Systema Naturae*, Gronovius became so impressed by the new classification method that he and his friend Isaac Lawton paid for its publication. It was

[2] Linnaeus, in Species Plantarum and elsewhere, cited Leonard Plukenet's *Cynoxylum americanum* (Plukenet, 1769, Vol. I, plate 172, fig. 6) as a synonym of *Nyssa*. Plukenet's sketch and description were first published in 1696, but they are insufficient for identification of the plant; therefore I have not given credence to the synonymy.

in this work that the name *Nyssa* was first applied to a genus of plants. Linnaeus placed the letter G. after the name, thus giving credit to Gronovius as its author, as he did in all of his subsequent systematic works. The name appeared next in Linnaeus' *Hortus Cliffortianus* (1737), where he stated that *Nyssa* was grown in George Clifford's garden from seeds supplied by Dr. Gronovius and that it had died the same year. No illustration of *Nyssa* was included in the *Hortus* but reference was made to Catesby's plate 41; therefore we know that Linnaeus considered this plant to be the same as Catesby's tupelo tree, even though he did not use the name which Catesby had given it. The *Nyssa* seeds which were unsuccessfully planted in Clifford's garden had surely been sent to Gronovius by John Clayton, for Gronovius later included two species of *Nyssa* in *Flora Virginica* (1739), his systematic treatment of Clayton's collections.

THE INTRODUCTION OF NYSSA INTO EUROPE

The first successful cultivation of an American *Nyssa* in the Old World took place in England, in the garden of Peter Collinson, a Quaker merchant of London. According to Aiton (1810-1813), *Nyssa denticulata* (= *uniflora*) was introduced by Collinson in 1735. Aiton's information regarding Collinson's garden came from Collinson's son, and is supported by evidence later discovered in the elder Collinson's catalogue of that garden (Dillwyn, ed., 1843). There are two species of *Nyssa* listed in the catalogue, however, each being referred to a different one of Mark Catesby's illustrations. I judge from Dillwyn's notes on the Collinson catalogue that *Nyssa sylvatica* and *Nyssa uniflora* were introduced at about the same time. Further evidence for this inference may be found in Aiton (1810-1813), where it is stated that a second species of *Nyssa* was "cult. 1739 by Mr. Ph. Miller", a friend of Collinson.

Peter Collinson is best known to us through his fond and fraternal correspondence with the Philadelphia plant collector John Bartram (Darlington, 1848). Beginning in the 1730's and continuing for a period of thirty years, Bartram supplied the merchant and his English acquaintances with specimens of every natural curiosity which could be boxed and put on a ship.

Collinson responded always with financial support, occasionally with straightforward advice on the management of Bartram's affairs, and eventually with the arrangement of Bartram's appointment as botanist to the king. Regarding his passion for collecting, Collinson confided to his friend, "My inclination to natural productions of all kinds is agreeable to the old proverb: *Like the parson's barn, — refuses nothing.*" (Darlington, p. 80) The Englishman was conversant with accounts of New World wonders written by Josselyn, Lawson, and others, and he frequently asked Bartram to collect curiosities which were mentioned in these accounts. It was probably the reading of Lawson's book which aroused Collinson's desire to see the plant called black or sour gum. On May 2, 1738, he wrote Bartram, "Pray forget not a specimen of the Black Gum in flower and in leaf for we are at a loss to know what it is." (Darlington, p. 118). Passages relating to this request which appear in Collinson's subsequent letters offer some solace to others of us who have wondered how *Nyssa* could possibly have acquired "gum" as a common name. The following excerpts are from Darlington, pp. 135, 143, and 152:

> June 10, 1740 . . . And please to remember a lump of Sweet Gum; Sour Gum; Allspice Gum if it bears any . . .
>
> July 21, 1741 . . . In answer to thine of December 4, 1740; and March 22 ult. The specimens of Sweet and Sour Gum I received; but I want the *Gum* of each sort. . . .
>
> March 3, 1742 . . . I thank thee for the Sweet Gum, or Liquid Ambar, as we call it . . . It is odd to call a plant sour Gum, or Black Gum, and it not produce any . . .[3]

Since Peter Collinson had introduced *Nyssa* into England in 1735, he must unknowingly have had a "black gum" under cultivation when he first asked for this plant from Bartram. Sometime after the requested specimens arrived, their identity was recognized, and Bartram was referred by Collinson to *Flora Virginica* for the name of the genus. The introduction date indicates that Collinson's first *Nyssa* seeds, like those planted in

[3] Sudworth and Mell (1911) have suggested that the name "gum" for *Nyssa* trees, none of which produces a gum, goes back to a time when all hollow trees might be used for hives and called "bee-gums" by country folk. I have encountered no evidence for or against such an explanation, but it is plain from Lawson's book, quoted in this article, that several quite different trees were called gums by early settlers.

George Clifford's garden, were supplied by Dr. Gronovius.

It is not known whether Clifford again planted *Nyssa* after his first attempt failed. That Nyssas were soon introduced successfully into Holland, however, is shown by the inclusion of an American *Nyssa* in the catalogue of the Utrecht Garden for the year 1747 (*fide* Wein, 1931). A century later the director of the Berlin Garden wrote that he had seen nyssas growing in many European gardens and that he himself had successfully cultivated four species (Otto, 1849).

DERIVATION OF THE NAME NYSSA

The reason that Gronovius and Linnaeus substituted the name *Nyssa* for Catesby's "tupelo" is not difficult to divine. We are informed by Linnaeus in his *Critica Botanica* (1737) that names which are barbarous in origin, he cannot accept (§ 229). Names of classical origin were quite acceptable, and *Nyssa* is such a name.

In attempting to explain the classical derivation of this word, dictionaries and botanical works have offered a variety of etymologies. According to *Webster's New International Dictionary* (1957), *Nyssa* is a Latinization of a Greek word meaning a goal or turning-post. A similar etymology is given by Dr. Roland Brown in his *Composition of Scientific Words* (1954). Other sources, including several botanical lexicons, list *Nyssa* as the name of a nymph. This nymph has been described as the nurse of Bacchus (Wittstein, 1852; *Century Dictionary and Cyclopedia*, 1911; *Funk & Wagnall's New Standard Dictionary*, 1935), or simply as a water-nymph (Beckmann, 1801; deTheis, 1810; Paxton, 1840; Gray, 1856), or both water-nymph *and* nurse of Bacchus (Lyons, 1900). There is even disagreement between the derivation given in Prof. Gray's *Field, Forest and Garden Botany* (1868), and that in his *Manual!*

Much of this etymological confusion is due to Gronovius' choice of an unusual spelling for Nysa, a word which appears occasionally in classical writings[4] as a personal name and as a geographical name (*Lexicon Totius Latinatis. Onomasticon,*

[4] I am grateful to Mr. G. Fitzgerald, Dept. of Comparative Literature, Harvard, for aid in locating and translating the Latin references cited in this paper.

1920). The Greek νυσσα indeed meant "a turning post", or "a goal" — it is used that way in the Iliad (Book 23, line 332) — but Gronovius had no such meaning in mind when naming his new genus. We may be sure of this, for *Nyssa* appears on the list of names of mythological deities retained by Linnaeus when he developed his system of nomenclature. In that list the name *Nyssa* is accompanied by the brief explanation *"Nyssa Nympharum una"* (*Critica*, § 237). Gronovius, who regularly read proof for Linnaeus' publications, would not have permitted such an explanation if it were not the correct one.

Etymologies describing *Nyssa* as the nurse of Bacchus are based on a brief passage by Diodorus of Sicily, a contemporary of Julius Caesar, who recorded several tales regarding the rearing of the motherless Dionysus (Bacchus). In one version, the infant is taken by his father Zeus to a city Nysa and given in charge of a girl Nysa. This Nysa is not a nymph, though, just "one of the daughters of Aristaeus" (Diodorus, 1935, book III, chapt. 70).

Nysa appears as the name of a nymph in the somewhat fragmentary fable number 182 of Hyginus (Rose, ed., 1934), probably written in the second century (*Oxford Classical Dictionary*, 1949). Here there are listed some Naiads, daughters of Oceanus, one of whom is named Nysa. Doubtless a classical scholar could cite additional uses of the name Nysa, but these should suffice to explain the multiplicity of meanings which have been attributed to *Nyssa* by our lexicons.

It would not be possible to choose between these somewhat obscure classical references, were it not for Linnaeus' statement that *Nyssa* means *"Nympharum una"*. Linnaeus also spared us from conjecture as to *why* these trees were named for a nymph, when he wrote in *Hortus Cliffortianus*, *"Nyssa dicitur cum in aquis crescat."* Not all nyssas are aquatic, to be sure, but neither Linnaeus nor Gronovius had seen the trees growing in their native habitat. They had before them, however, the two polynomials previously applied to Catesby's tupelos, each of which began, *"Arbor in aqua nascens . . ."* In short, the explanation given in Gray's *Manual*, that *Nyssa* is named for a nymph be-

cause it grows in the water, is the correct one, being taken from Linnaeus' own explanatory remarks. — *Department of Biology, Harvard University.*

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A NEW PEPEROMIA FROM JAMAICA. — Botanical exploration in the John Crow Mountains of eastern Jamaica has brought to light new species of plants in nearly every family of plants occurring in the area, suggesting a long history of at least ecological isolation from the rest of the island. Among the undescribed species collected in recent years is the following diminutive *Peperomia,* which has been found several times on the sheltered sides of overhanging limestone cliffs.

Peperomia lewisii Proctor, sp. nov.

Herba parva et fragilis; caulibus breve pilosis, plerumque sine ramis, recurvato-pendentibus, 3–8 cm. longis, non plus quam 1 mm. diametro. Foliae oppositae vel paucae alternatae 1.5–2 (–2.5) cm. longae, includenti petiolum gracile 3–4 mm. longum, lamina obovato-elliptica, apice rotundata, base cuneata, 0.5–1 cm. lata; supra glabrosa praeter prope marginem, griseo-virida vivens, tenebrosior sicca; infra hispidulosa, pallide-virida vel punicea. Spicae 1–3, terminales vel solae in axillis superioribus, graciles, glabrosae, 1–3 cm. longae; pedunculi hispidulosi, circa 8 mm. longi; drupae circa 0.5 mm. diametro, fuscae sicca.

Small, fragile herb; stems short-pilose, mostly unbranched, recurved-pendent, 3–8 cm. long, not more than 1 mm. in diameter. Leaves opposite or a few alternate, 1.5–2 (–2.5) cm. long (including the slender, 3–4 mm. long petiole), the blade ovate-elliptic, apex rounded, base cuneate, 0.5–1 cm. broad; upper surface glabrous except near the mar-

gin, gray-green when fresh, darker when dry; lower surface hispidulous, pale green or pinkish. Spikes 1–3, terminal, or solitary in the upper axils, slender, glabrous, 1–3 cm. long; peduncles hispidulous, about 8 mm. long; fruits about 0.5 mm. in diameter, dark brown when dry.

TYPE: Parish of Portland, east slope of the John Crow Mountains 1.5–2.5 miles southwest of Ecclesdown, on shaded limestone cliff, elevation 1500–2500 ft., *Proctor 10473*, collected August 11, 1955 (Holotype at the Institute of Jamaica). Additional material: *Proctor 9996* and *Webster & Wilson 5148*, from the same general area.

Named for Mr. C. Bernard Lewis, Director of the Institute of Jamaica and Curator of its Museum.

This species somewhat resembles *P. barbata* of the Jamaican "Cockpit Country" and adjacent areas, but differs in its much slenderer, mostly unbranched, recurved-pendent stems, its obovate-elliptic (instead of roundish-elliptic) leaves of more delicate texture, by its glabrate upper leaf-surfaces, and by its slenderer, shorter spikes and smaller fruits.

P. lewisii also differs from *P. spathophylla* Dahlst. of eastern Cuba (with which it was for a time confused) in its short-recurved (instead of long-creeping) stems which are never stoloniferous, its mostly opposite (instead of alternate) leaves which are glabrate above and never retuse or retuse-cordate, in its hispidulous (instead of glabrous) peduncles, and in having slenderer spikes. The fruits of the two species cannot at present be compared because those of *P. spathophylla* are known only in an immature state.—GEORGE R. PROCTOR, INSTITUTE OF JAMAICA, KINGSTON, W. I.

VIOLA ERIOCARPA VS. V. PENSYLVANICA. — The two common widespread, yellow-flowered, leafy-stemmed violets in eastern North America, *Viola pubescens* and *V. eriocarpa* are readily distinguishable by several morphological characters. Their taxonomy and ecology seem to be adequately understood, but on one point of nomenclature a correction seems to be necessary, as in recent years a few sporadic attempts have been made to substitute for the well-known binomial *Viola eriocarpa* that has stood since 1822, another that has been supposed to antedate it, namely *V. pensylvanica* Michaux (1803).

As already noted, the two species of violets are clearly defined.

Plants of *Viola pubescens*, described by Aiton in 1789, are decidedly pubescent, with strongly veined thickish leaves with ovate stipules, the basal leaves usually absent at flowering time, and seeds 2.6-3 mm. long. The other species of this pair, described by Schweinitz in 1822 from North Carolina as *V. eriocarpa*, is nearly glabrous, with thinner, less conspicuously veiny leaves, and somewhat narrower stipules, the basal leaves usually present at flowering time, and smaller seeds about 2-2.6 mm. long.

In 1941 an attempt was made (Rhodora 43: 616-617) to displace the name *V. eriocarpa* in favor of *V. pensylvanica* Michx. An argument was presented that a photograph of the original material of Michaux's *V. pensylvanica* shows a mixture of *V. pubescens* and of *V. eriocarpa*, the former represented by very immature plants scarcely in bloom, the latter by a plant with well-grown foliage and an old flower. The author concludes that the latter stands as the type of the Michaux name. When we turn, however, to the original description we find the statement "V [iola] tota villoso-pubescens": the conclusion seems inescapable that the plant described is *V. pubescens* Ait. According to Recommendation 8C (Int. Code, 1956), whenever type material of a taxon is heterogeneous, the lectotype should be so selected as to preserve current usage unless another element agrees better with the original description and (or) figure, and in Appendix IV, paragraph 4, "The original description of the taxon concerned should be the basic guide."

That part of the original material of *Viola pensylvanica* that agrees with the original description in Michaux's Flora Boreali-Americana 2:149 (1803) is designated as the lectotype, and *V. pensylvanica* is clearly a synonym of *V. pubescens*. — GEORGE NEVILLE JONES, UNIVERSITY OF ILLINOIS.

THE TYPE OF SETARIA FABERII. — The majority of plant taxonomists regard *Setaria faberii* Herrmann as a distinct species. A noteworthy exception is H. A. Gleason. In December, 1953 he wrote to me "I frankly can not see *S. faberii* as a good species. To me it is just another race of *S. viridis*, to be recognized possibly as a variety, or a form, or what you please, but to me it is not a species." The absence of the taxon from his New Illustrated

Flora was no oversight but the result of courageous deliberate exclusion. David E. Fairbrothers (Brittonia 11: 44-48. 1959) has brought the full force of his attention to the subject of morphological variation of *S. faberii* and *S. viridis*. After measurements and observation of numerous plants both from wild populations and cultivation he defined comparative sizes in the spikelets, panicles and bristles for the two species, which he set in a key, and furthermore concluded that: "The one stable qualitative feature was the strigose condition of the upper surface of the blades of *S. faberii* in contrast to the glabrous or glabrate condition present in *S. viridis*." Although Dr. Fairbrothers did not definitely state whether he accepts *S. faberii* in the specific category, his treatment would seem to suggest so. The investigator did not study the species on a world-wide basis; he apparently consulted few herbaria, and did not examine the type of *S. faberii*. Because of the latter omission there arises a peculiar situation regarding "the one stable" feature, leaf-pilosity, a dilemma which will be discussed below. The principal purpose of the present note is to indicate the problem of pilosity of the leaf-blades of *S. faberii* especially in the light of the type of the species.

For several years I have given some cursory attention to *S. faberii*. The species grew in vast quantities, almost like a cultivated crop, on the grounds in the rear of the Museum Building of The New York Botanical Garden. A specimen (Monachino #582) was sent to Jason R. Swallen in October, 1953, who confirmed the identification and asserted that he considered *S. faberii* "a good species." This collection has hairy leaf blades. The pilosity on the upperside of the leaf blades of *S. faberii* is easily observable; it can be clearly seen, and even felt by merely running the fingers lightly over the surface of the blade. The very ease with which this character is employed (I suspect) has sometimes prejudiced my identification in doubtful cases. It is thus that I refrain from naming another of my collection from The New York Botanical Garden grounds (Monachino #583, Sept. 1956), notwithstanding that measurements would key it out to *S. faberii* and that it was growing in a population

of *S. faberii* and simulating that species. The spikelets of my #583 are over 2.5 mm. long, the length of the panicle is up to 10 cm. and its width up to 8 mm.; the sterile lemma of the spikelet manifestly surpasses the second glume. The maxima given for *S. viridis* by Fairbrothers are 2.2 mm., 9.5 cm. and 0.7 cm., respectively; sterile lemma length ratio to 2nd glume 0.95 to 1.06. The leaf blades of #583 are glabrous and so it lacks Fairbrothers' one stable qualitative feature conveniently characterizing *S.faberii.*

My specimen #583 is not the only one in the herbarium of The New York Botanical Garden with glabrous blades and with measurements surpassing those given for *S. viridis.* A Chinese collection distributed as *S. viridis* is another example: *Steward Chiao & Cheo 220,* Kweichow Province, Liang Feng Yah, Tsunyi Hsien, 6 Aug. 1931. Fernald in the 8th edition Grays' Manual describes the spikelets of *S. viridis* up to 2.5 mm. long.

As to the constancy of leaf-strigosity of *S. faberii,* Fernald said "usually", and I have examined plants having lower leaves manifestly pilose while the upper ones were glabrous. But the most disconcerting problem concerning pilosity is posed by the very type of *S. faberii.*

In the original description of *S. faberii,* Herrmann (Beitr. Biol. Pfl. 10; 51. 1910) described the leaves glabrous above: "laminis utrimque glabris, supra scabris." The type was collected in China, Szech-uen, Faber No. 582–1182, and at Vienna. A specimen of Faber 1182, possibly an isotype, is found amongst specimens of *S. viridis* in the herbarium of The New York Botanical Garden, has glabrous blades. Through the kindness of Karl H. Rechinger, Naturhistorisches Museum, Wien, I obtained a portion of a leaf from the type and this too is glabrous! Apparently the type lacks the very feature named constant for the species!

It is thus seen that the problem centering on *S. viridis* - *S. faberii* is a complex one indeed, at least regarding pubescence. How is one to harmonize Fairbrothers' conclusion concerning leaf-pilosity with the type of *S. faberii?* Dr. Fairbrothers, who has read this paper in manuscript, provides part of the answer him-

self. He wrote to me (letter of 27 April 1959): "Since my *Setaria* paper appeared in Brittonia specimens have been sent to me by taxonomists from three different states in which the five quantitative characteristics fit *faberii*, but the leaves were glabrous. Each person indicated they found only one or two plants of the glabrous type in a population of hairy ones." — JOSEPH MONACHINO, NEW YORK BOTANICAL GARDEN.

AN INTERPRETATION OF TWO FORMS OF OSMUNDA CINNAMOMEA

TAYLOR A. STEEVES

Within the range of Gray's Manual, six aberrant forms of the cinnamon fern, *Osmunda cinnamomea* L., have been described, in addition to the typical form and the well defined var. *glandulosa* Waters. Other varieties are also known from tropical and sub-tropical America and from eastern Asia. The writer and several of his colleagues have been interested in this species for over ten years as a remarkably fine subject for morphogenetic studies. During this period many observations have been made on plants growing under natural conditions in the vicinity of Boston, Massachusetts, and certain tagged plants have been examined in successive growing seasons. These studies have made it possible to offer at least partial explanations for two of the described forms, forma *frondosa* (T. & G.) Britt., and forma *latipinnula* Blake.

O. cinnamomea, f. *frondosa* was first described as a variety by Torrey and Gray (Torrey, 1840), and later reduced to a form by Britton (1890). In contrast to the typical condition in which fertile fronds are completely distinct from foliage fronds and are without laminar development, this form is characterized by reproductive fronds which bear some laminar tissue. In fact, sterile pinnae may predominate, with only a few sporangia-bearing leaflets present. The fertile and sterile pinnae are variously intermixed; and sometimes sporangia may even be born on the edges or backs of leafy pinnae. In the writer's own observations, the sterile pinnae have been basally located and have given way, with various intermediates, to fertile pinnae in

the upper portion of the frond in the manner reported in the original description of the phenomenon (Torry, 1840). Other arrangements, however, can occur (Kittredge, 1941). There have been well-documented suggestions that this form represents a response to unusual environmental conditions such as burning (McLouth, 1897), a late spring frost (Owen, 1901), or the close proximity of a recently tarred roadway (House, 1933); but still the form with its Latin name has persisted.

It is evident from regular observations of tagged plants in the field, that there is considerable variation from year to year in the number of fertile fronds produced by any given plant. For example, one group of 19 plants, which was treated as a unit, produced a total of four fertile fronds in 1949, and in 1950 produced 25. Although fertile fronds are not evident above ground until early spring, it is known (Steeves and Wetmore, 1953) that the nature of the leaves is fully determined within the apical bud during the preceding season. Dissections in late summer show that the fertile fronds for the next year are fully formed, but coiled, and that the sporangia are present. It would seem reasonable to suppose that environmental conditions during the period of frond determination might influence the extent of fertility in any plant. No real evidence is available on this matter, but two observations may be reported. It has been noted that a hot dry summer is usually followed by a high degree of fertility in the following spring, whereas a cooler, moister summer leads to reduced fertility. Further, a comparison made in one area between plants in heavy woods and plants in a powerline right-of-way revealed a consistently higher level of fertility in the open right-of-way. Such observations suggest that temperature, soil moisture, or possibly total light energy received might be important factors in regulating the extent of fertility. Recent studies (Sussex and Steeves, 1958) on excised leaves of several species of ferns, including *O. cinnamomea*, growing in sterile nutrient culture, have shown that an increased supply of carbohydrate favors the initiation of sporangia; but it is difficult to correlate such observations with environmental conditions in the field.

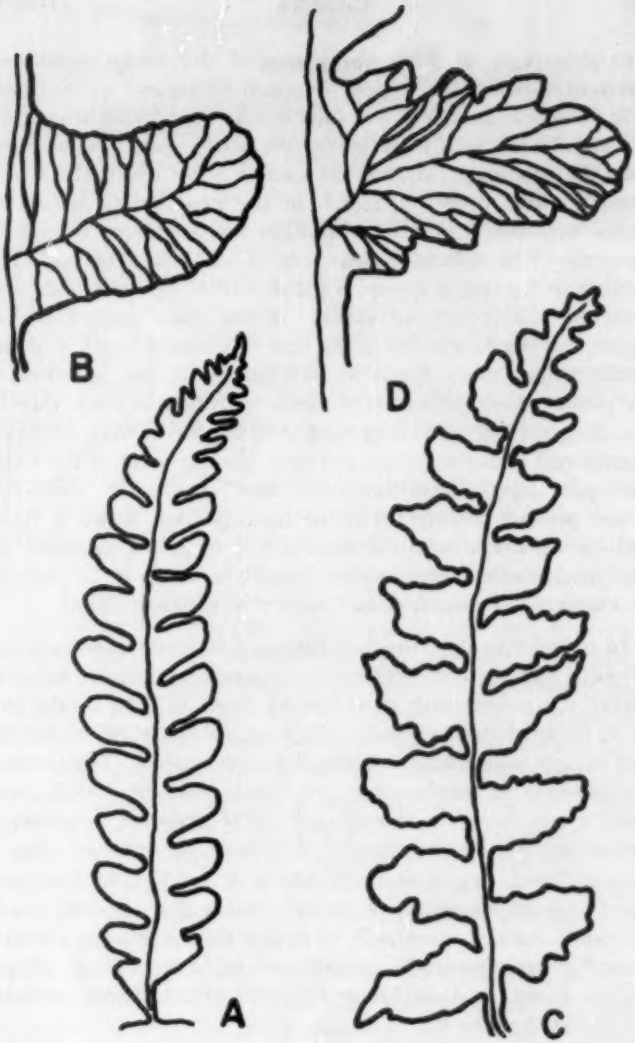

FIG. 1. A comparison of single pinnae (A and C) and single pinnules (B and D) from a typical example of *O. cinnamomea* (A and B) and from an example of *O. cinnamomea* f. *latipinnula* (C and D). A and C natural size. B and D X 4.

In the spring of 1949, the plants of the group mentioned above were all normal, that is, no mixed fertile and sterile fronds were observed. In 1950 three such fronds were found among the 25 fertile fronds produced, two on one plant, which also bore two normal fertile leaves, and one on another plant which also bore a normal fertile frond. A search of the neighboring woods revealed that the "frondosa" condition was common throughout the area. The following year was characterized by moderate fertility in the tagged group of plants and no mixed fronds were observed. As mentioned earlier, in the cases studied by the writer, the sterile portion of the leaf was always basal, with the fertile pinnae more apical in location. Since the initiation of the pinnae along the rachis proceeds from base to apex (Steeves and Briggs, 1958), it is suggested that the leaves were originally determined as sterile fronds and then changed over to the fertile condition after pinna initiation had begun. In individual mixed pinnae, however, it is the basal portion which is fertile and the tip sterile; and the same is true of mixed pinnules. An explanation of this phenomenon cannot as yet be given since the development of pinnae is not known in sufficient detail.

In contrast to the form just discussed, *O. cinnamomea* f. *latipinnula* Blake is both striking in appearance and rare in occurrence. It was originally described by Blake in 1913 on the basis of its broad, deltoid pinnules which are characterized by a crenulate margin which may even become faintly lobed. The pinnules are reduced in number and are correspondingly broad (more than a centimeter in some cases). The venation is unusually coarse and the lateral veinlets are more pronounced than in normal fronds (fig. 1, cf A and B with C and D). In many ways the fronds are suggestive of juvenile leaves of the species except, of course, for size. Originally described from Vermont, f. *latipinnula* has subsequently been collected in Massachusetts (Report on the Flora of Massachusets II, 1933), Pennsylvania (Gruber, 1940) and New York.

In the early summer of 1951, three plants of f. *latipinnula* were found by the writer, growing through a pile of brush on

a powerline right-of-way in Hingham, Massachusetts. The identity of the material was established by Prof. W. H. Wagner, Jr., who also ascertained that there was no polyploidy involved in this unusual vegetative form. The fronds were late in emerging from the apical bud and were very slender and weak. Two of the abnormal plants were carefully marked, and a third was taken to the laboratory in the fall and stored over winter in a cold room. In the following spring, this plant was forced in a greenhouse. This plant, as well as the two left in the field, were of essentially normal form, although the fronds showed some slight deviation from the typical condition. In any event they were not of the *latipinnula* type. Clearly then f. *latipinnula* is a temporary condition representing a modification of normal leaf development.

It seemed at least possible that the heavy covering of brush had in some way induced these abnormal characteristics. Accordingly, in the fall of the year, several tagged normal plants were covered by similar piles of brush. These plants were examined in the following spring and found to be essentially normal. The fronds grew through the covering with difficulty, and were somewhat distorted; but they did not show the *latipinnula* characteristics. In late summer of 1951 a large-scale experiment was performed, to the writer's benefit but not at his instigation, which shed much more light upon the nature of this aberrant form. The powerline right-of-way was cleared again and new poles were set. These operations involved the bringing of considerable heavy equipment into the area. The following spring, a number of new examples of f. *latipinnula* were discovered in the cleared area. They were of the same form as the previous examples, but the fronds were not weak. Furthermore, there was no covering of brush over them.

There was now sufficient material available to make it possible to dissect some of the plants in an attempt to ascertain the cause of the abnormality. In all cases there was definite evidence of injury to the plant, and many leaf bases showed the results of breaking or crushing. Two plants, located side-by-side, were especially enlightening in this connection. Both were in the path

of a truck tire track, and both were of the *latipinnula* type. Examination of the plants which had been found during the previous season also gave clear evidence of injury, presumbly in an earlier clearing operation. It thus seemed reasonably established that the f. *latipinnula* is a response to rather drastic injury. It was, moreover, possible to establish the role which the injury had played.

Previous studies (Steeves and Wetmore, 1953, Steeves and Briggs, 1958) have shown that *O. cinnamomea* is characterized by a slow rate of leaf development. Leaves are produced at the shoot apex and develop within the apical bud for nearly four years before finally expanding above ground. As a consequence, the apical bud contains a large reservoir or pool of immature leaves, sufficient throughout most of the year for four subsequent growing seasons. During the growing season preceding final expansion of an annual set of fronds, the leaves of this set acquire the form of cataphylls (bud scales), fertile fronds and sterile fronds; and, starting from the outside of the bud, this is the sequence of leaf types within each set. Both fertile and sterile fronds form a rachis with pinnae, coiled into the characteristic fern crozier. The cataphylls, on the other hand, develop a flaring margin on the leaf base, but the portion which in the other leaves develops into the above-ground portion, is arrested in its growth and does not complete its development. During the winter, the cataphylls enclose and protect the apical bud. In the spring the fertile and sterile fronds push up inside these and expand above ground. Then a new set of cataphylls, fertile fronds and sterile fronds begins to take form from immature leaves inside these. Also, at the very center of the bud, a new set of primordia is added to the reservoir by the apical meristem. In other words, each year one set of leaves is used up at the outside of the bud and a new set is added at the center, so that the number of sets in the pool remains relatively constant. The cataphylls early lose any power to develop a complete rachis with pinnae because the leaf apex stops growing and usually undergoes necrosis. This loss progresses from the outside of the set inwards, but ends abruptly with the first frond, the apex of

which is actively developing. Early in the growing season, the removal of the current year's set of fronds has the effect of forcing some of the cataphylls to expand above ground. If this operation is performed somewhat later, the outer cataphylls will not respond, but some of the inner ones which have not lost the power of apical growth may do so. After early July, there is ordinarily no response at all; but sometimes a drastic treatment, such as complete mowing of a large area, will cause some of the innermost cataphylls, or even some of the next season's fronds, to complete their development and expand. Under these conditions, the fronds which emerge may be abnormal, and many show a broadening of the pinnae suggestive of the f. *latipinnula*. They are not, however, typical examples of this form.

In the case of the plants which showed *latipinnula* characteristics in 1952, the situation was somewhat more complex; but an examination of the cataphylls and persistent leaf bases outside the fronds of the current year has made an interpretation possible. In the latter part of July of 1951, the area was cleared and all fronds were mowed down. In many plants, probably including those under consideration, some of the inner cataphylls began to develop as fronds. The fronds for the next growing season continued to develop their croziers or a few may have started to form cataphylls. Then, later in the summer, an injury occurred which destroyed not only the released cataphylls, but also the fronds for the next growing season and possibly some leaves inside them. Subsequent developments are not very clear; but it appears that a new set of cataphylls was formed inside the crushed fronds, and that inside these a new set of fronds developed for the next season. In fact, the cataphylls and new fronds were, to a certain extent, intermixed, a condition never found in normal plants. When these new fronds expanded during the following spring they were of the *latipinnula* form.

In essence, the injury, occurring when it did, pushed the entire leaf utilization sequence considerably further into the special bud than is normal. The *latipinnula* fronds developed, therefore, much more rapidly than under normal circumstances. It is suggested that the drastic change of form of these fronds was

the result of this accelerated development. The tendency toward the *latipinnula* condition in fronds forced by mowing in late summer provides support for this interpretation. Changes in leaf form resulting from acceleration of development have been noted previously and have been described in detail in certain woody dicotyledons by Späth (1912). In any event, the f. *latipinnula*, like the f. *frondosa*, has no genetic or taxonomic significance, but should rather be regarded as one of the variable morphogenetic expressions of the leaf of *O. cinnamomea*.

It is a pleasure to acknowledge the valuable assistance of Mr. C. P. Steeves and Mr. G. S. Lord in making field observations and in reconstructing the history of the area in which they were made, and to Prof. W. H. Wagner, Jr. for his helpful advice and suggestions. Miss Barbara Coffin very kindly drew the illustrations in Fig. 1. — DEPARTMENT OF BIOLOGY, UNIVERSITY OF SASKATCHEWAN, SASKATOON, SASK.

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